CHAPTER 2

ACTIVITY PATTERNS OF MARBLED MURRELETS IN DOUGLAS-FIR OLD-GROWTH FORESTS OF THE OREGON COAST RANGE

ABSTRACT

Activity patterns of Marbled Murrelets (*Brachyramphus marmoratus*) were monitored on a near-daily basis during three breeding seasons at five inland forest sites in the Oregon Coast Range. Four daily activity metrics (numbers of daily detections, vocalizations, occupied detections, and duration of daily activity) were monitored and each was highly variable within and among sites and years. We observed greater variability in activity levels than has been previously reported for this species. We could not identify any month when coefficients of variation for activity metrics were consistently higher or lower than any other month. Activity metrics tended to be strongly correlated within a day within survey stations, but correlative relationships at temporal and spatial scales greater than this were inconsistent and moderate at best. Marbled Murrelet activity varied greatly from one day to the next during all portions of the breeding season and multivariate analyses revealed that weather and date variates explained little of the variability present. Given the extreme levels of variability in Marbled Murrelet activity and our lack of understanding as to which factors drive that variability, it is critical that biologists not draw conclusions about activity or behavior from small data sets or data sets not specifically designed to answer the questions of interest.

INTRODUCTION

Daily or near-daily surveys of seabird colony attendance have revealed important aspects of species' breeding biology, foraging ecology and social behavior, and have been used to determine environmental factors that affect attendance patterns, interpret seasonal activity patterns, and design monitoring plans (e.g., Byrd et al. 1983, Gaston and Nettleship 1982, Hatch and Hatch 1988 and 1989, Jones et al. 1990). However, such survey efforts are rare for Marbled Murrelets (*Brachyramphus marmoratus*), a threatened alcid that typically nests in coastal or near-coastal, old-growth, coniferous forests throughout much of its range in the Pacific Northwest (PNW) of North America. Instead, interest in assessing the loss of and disturbance to nesting habitat from timber management activities has given rise to a survey protocol designed to determine probable nesting status in forest stands (Ralph et al. 1994). For example, this protocol requires 4 surveys / breeding season for at least two years to produce a 95% probability of detecting birds if they are present. Observations of birds during surveys are referred to as 'detections' and are defined as "the sighting or hearing of one or more Murrelets acting in a similar manner" (Ralph et al. 1994). Nesting status is then predicted based on the types of detections observed. The numbers of detections recorded during a survey or series of surveys does not correspond directly to the numbers of birds using a particular forest stand, however. For example, it is likely that both double-counting and omission of birds occurs during surveys. Nonetheless, the quantitative relationship between numbers of detections (i.e., activity) and numbers of nesting birds is assumed to be positive.

Recently, counts of detections from Marbled Murrelet surveys have been used for quantitative analyses. For example, daily detection data have been used to compare activity levels among habitat types, describe seasonal attendance patterns, and monitor temporal trends in activity over time (see Ralph et al. 1995b for examples). However, daily counts of detections tend to exhibit a high degree of seasonal variability within and among stands (Naslund and O'Donnell 1995, O'Donnell et al. 1995) and there is an insufficient understanding of the factors that may be causing such high variability. Furthermore, most stands receive low survey effort each year (e.g., 4 surveys / year; Ralph et al. 1994). This suggests that conclusions drawn from quantitative analyses of detection data may be misleading. Three other daily activity metrics also are recorded; number of vocalizations, number of occupied detections (a detection which infers a high probability of birds nesting in the stand based on observed behavior), and duration of activity during the daily survey period. However, the interrelationship of all four daily activity metrics and the levels of variability for each are not fully understood and therefore their potential use as quantitative metrics of activity is unknown.

The goal of this study was to examine activity patterns (i.e., the four metrics previously mentioned) of Marbled Murrelets in the Oregon Coast Range and obtain improved estimates of the variability in activity data and its relationships with both local weather and date. The objectives were to: (1) examine the correlative relationships among the four activity metrics at multiple temporal scales; (2) examine the relationship between weather at the stand and the daily activity metrics; (3) examine activity patterns on a daily, weekly, seasonal, and inter-annual time scale; (4) quantify the variability occurring in the primary survey metric, counts of daily detections, and examine factors that might influence that variability; and (5) describe flight behavior of Marbled Murrelets observed during surveys and determine influential factors. This study significantly extends the quantity of information available on Marbled Murrelet activity patterns; the number of surveys conducted at each station each year during this study were greater than any previously reported for this species throughout its range.

METHODS

Study Sites

Five survey stations are located in Douglas-fir (*Pseudotsuga menziesii*) old-growth forests in the central Oregon Coast Range (Figure 2.1). The Valley of the Giants Meadow (VGM; 365 m ASL) and Valley of the Giants Upper Plateau (VGUP; 535 m ASL) survey stations are 25 km inland and 2 km apart. Marbled Murrelet nests have been located in each of these stands (Hamer and Nelson 1995). The Spencer Creek Main Fork (SCMF; 100 m ASL) and Spencer Creek Upper Fork (SCUF; 100 m ASL) stations are 23 km inland and 1.5 km apart. The 2x4 station (425 m ASL) is 25 km inland. All survey stations are in the Coast Range Province and western hemlock (*Tsuga heterophylla*) vegetation zone (Franklin and Dyrness 1988), and are managed by the Bureau of Land Management (BLM). None have been harvested and all but VGUP are located along rivers or creeks. All stands are within a mosaic of the western hemlock habitat type, with surrounding stands varying in age. Survey stations located in the same area (i.e., VGM and VGUP, SCMF and SCUF) are hereafter referred to as proximal survey stations.

Field Techniques

We monitored Marbled Murrelet activity during the breeding season by conducting a minimum of 50 daily surveys/station/breeding season. Murrelet surveys began 45 minutes prior to sunrise and ended 75 minutes after sunrise, or 15 minutes after the last detection, whichever was later. Surveys were conducted between 1 May and 4 August

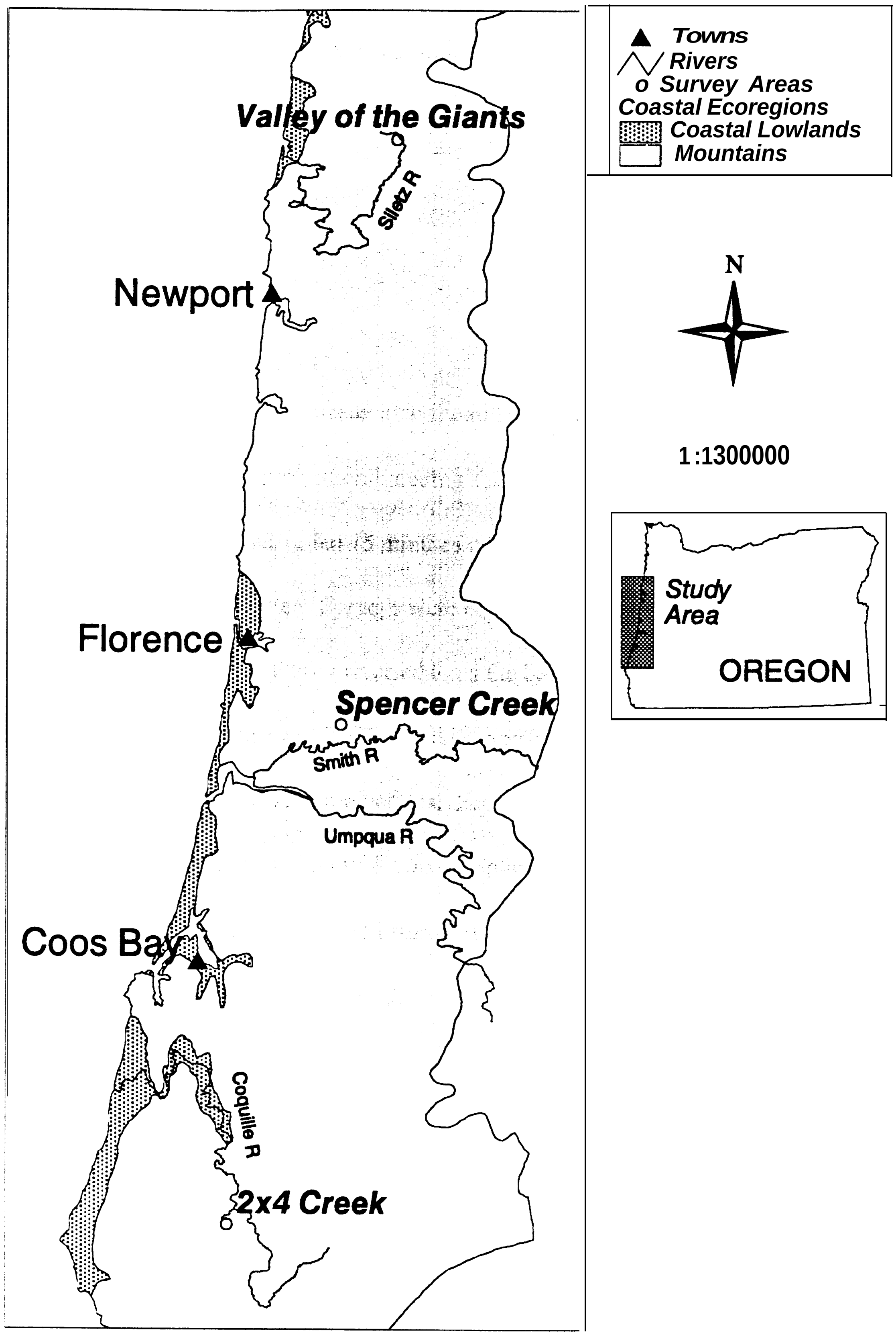


Figure 2.1. Marbled Murrelet survey areas, Oregon Coast Range.

(95 possible survey days hereafter referred to as the breeding season) in 1994 (VGM, VGUP, SCMF, SCUF), in 1996 (VGM, VGUP) and in 1997 (VGM, VGUP, SCMF, 2x4), resulting in 10 site*year combinations. Each station was surveyed by the same observer during a breeding season with two exceptions, VGM 1996 and SCMF 1997. For these two situations, we conducted simultaneous surveys with the original and replacement surveyor. Results (daily tallies of each activity metric and timing of observed detections) from these simultaneous surveys were similar. All surveyors were trained prior to data collection..

For each detection observed during a survey we also recorded: time of day; type of detection as silent-visual, audio-visual, or audio only; and number of 'keer' calls (the primary vocalization). For visual detections we additionally recorded height of birds in relation to the canopy; behavior of birds (categorized as flying over canopy in a straight line, circling over canopy, circling below the canopy, flying through or below the canopy in a straight line, landing in or departing from tree, or stationary); and group size. All detections were categorized as 'occupied' or 'present' based on observed behaviors (Ralph et al. 1994). Detections in the 'occupied' category are more indicative of nesting and include visual observations of birds below the canopy as well as birds circling above the canopy. Detections in the 'present' category indicate birds occur in or around the forest stand and include visual observations of birds flying in a straight line over the canopy as well as all non-visual detections. Daily survey data were summarized by calculating the duration of activity in minutes (duration = time of last detection - time of first detection) and tallying the numbers of detections (occupied and present combined), occupied detections, and keer calls. These four metrics are hereafter referred to as the daily activity metrics.

We recorded weather variables every 20 minutes during murrelet surveys. Cloud and fog cover were each estimated to the nearest 25%. Height of cloud ceiling was estimated relative to the forest canopy so that measurements from all stands would be comparable.

Ceiling below canopy was recorded as <1 and ceiling above canopy was estimated to the nearest multiple of the canopy height, up to 5. Precipitation was categorized as none, drizzle or mist, steady rain or down pour. Wind was recorded on a modified Beaufort scale. Data on each of the weather variables were averaged for each survey day to create a daily summary value.

Statistical Analyses

Relationships between activity and both weather and date.—Canonical correlation analysis was used to examine the relationship between Marbled Murrelet activity and both date (month and year) and weather. This multivariate approach was used because all activity metrics were strongly correlated (Spearman correlation (r_s) coefficients > 0.7). Canonical correlation is an extension of multiple regression that examines the linear relationship between multiple X and Y variables by creating linear combinations (i.e., variates) for each data set that best express the correlation between the two data sets. The first canonical correlation explains the maximum relationship between the canonical variates and each successive canonical correlation is estimated so as to be orthogonal yet still explain the maximum relationship not accounted for by the previous canonical correlation. The overall strength of the relationship between the X's and Y's is assessed by examining canonical correlation coefficients (CC) and canonical redundancy indices (CRI); the latter measures the average proportion of variance in the Y variables explained by the X variables. A more detailed examination of the canonical correlation structure may be accomplished by examining canonical loadings (CL) and canonical cross-loadings (CXL). CLs estimate the influence of each independent variable on the newly created variate, and CXLs estimate the strength of the correlation between each dependent variable and the independent variate set (Hair et al. 1995).

The number of daily occupied detections could not be transformed to meet the assumptions of canonical correlation. Spearman correlations were used to assess the relationship between the number of daily occupied detections and CLCEFO. Kruskal-Wallis analyses were used to examine the effect of month, year, and site on the number of daily occupied detections. Additionally, multicollinearity among the dependent variables cloud cover, ceiling, and fog prevented each from being included in the canonical correlation analysis. We used principal components analysis to assess the relationship between the weather variables and determined that cloud, ceiling, and fog each weighted the first principal component evenly. Therefore, we created a new variable, termed CLCEFO, by summing the daily standardized values of each of these three metrics (Hair et al. 1995).

We also used locally weighted regression and smoothing scatterplots (LOWESS) to check for nonlinear relationships between activity and date, since canonical correlation is restricted to seeking linear trends. Counts of daily detections were plotted as the smoothed proportion of the maximum daily detection count (for LOWESS plots only) to standardize measures among stations

Behavior during detections.—We used generalized linear models to investigate relationships among Marbled Murrelet flight behaviors, date, and time of day; these analyses were performed on visual detections only. Group size, a nominal variable representing the number of murrelets flying together in a detection (range 1 to 8), was analyzed with Poisson regression. Explanatory variables available for inclusion in the model were time of day (categorized by 20 minute blocks beginning at the start of the survey period and labeled as time periods 1 - 6), month, height of birds detected in relation to the canopy (above or below canopy), detection type (silent visual or audio visual), and all possible second-order interaction terms. We ran three separate Poisson regression models in an effort to keep the data relatively balanced among years and sites. We included survey data from VGM and VGUP in 1994, 1996, and 1997 in the VG model; data from SCMF and SCUF in 1994 in the SC model; and data from 2x4 in 1997 in the 2x4 model. We used a forward, single-best-predictor process with an F-to-enter value of 4.0 to select significant explanatory variables. Final models were then chosen based on a combination of drop-in-deviance tests and Bayesian information criteria. Mean responses are presented for Poisson regression models. In situations where mean responses < 1 were calculated, we used the inverse (i.e., positive interpretation) of the value to present a more meaningful statistic. Due to restrictions of degrees of freedom, only a limited number of comparisons among categories of explanatory variables could be made in Poisson regression models; these are presented in the summary tables for each model. August detection data were not used in canonical correlation, Kruskal-Wallis, or generalized linear models since sample sizes from that month were <5.

RESULTS

Survey Effort and Summary Statistics

We conducted 572 daily surveys for Marbled Murrelets, averaging 57.2 survey days/station/year. Most detections occurred within +30 minutes of sunrise (e.g., Fig. 2.2). At least 1 Marbled Murrelet detection was recorded on 517 mornings, although 7 of 10 site*year combinations had at least one day with no detections. We recorded 13,259 detections (36% were classified as occupied), approximately 104,000 keer calls, and 25,058 minutes of activity (Table 2.1). Approximately 55% of all detections were strictly audio, although this proportion varied within and among sites and years (Table 2.2). A total of 10,848 Marbled Murrelets were sighted during 4,148 silent-visual and 1,840 audio-visual detections. The proportion of detections that were silent-visual was greater than the proportion that were audio-visual at each site each year (Table 2.2). The maxi-

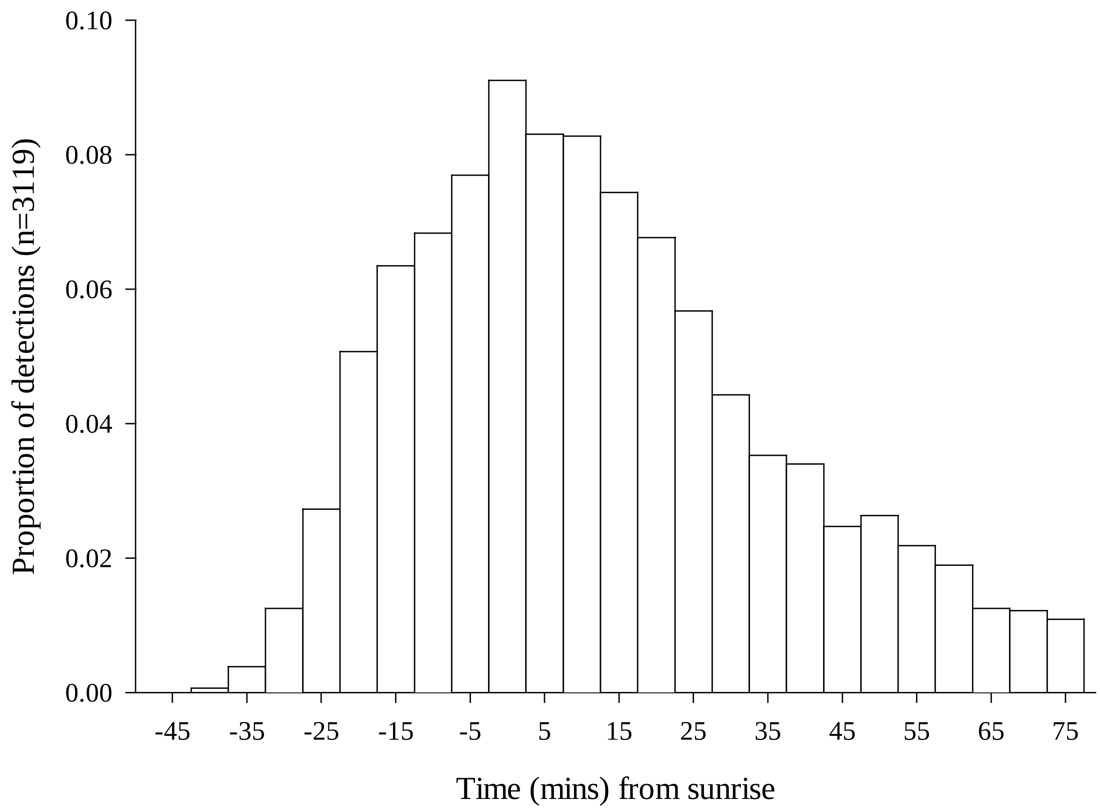


Figure 2.2. Proportion of Marbled Murrelet detections recorded by time of day in relation to sunrise during standrad survey hours at the 2x4 survey station, Oregon Coast Range, 1 May - 5 August, 1997. Detections recorded >75 minutes post sunrise (n = 131) not included due to unequal sampling effort during those hours.

Table 2.1. Summary statistics from Marbled Murrelet surveys for daily counts of detections, keer calls and duration of activity (minutes) at five survey stations, Oregon Coast Range, 1 May - 5 August 1994, 1996, 1997. n = number of survey days.

	Survey stations									
	2x4	SCMF		SCUF	VGM			VGUP		
Metric statistic	‘97 (n=62)	‘94 (n=66)	‘97 (n=61)	‘94 (n=58)	‘94 (n=55)	‘96 (n=50)	‘97 (n=58)	‘94 (n=55)	‘96 (n=51)	‘97 (n=56)
Detections										
mean/day	51.29	32.45	10.56	16.22	27.31	7.66	15.29	36.14	14.10	14.69
min/max	2/147	0/198	0/83	0/112	0/79	0/38	1/56	1/88	0/39	0/85
CV	69.51	130.00	152.46	134.08	68.40	113.43	87.44	49.30	72.09	121.65
Keer calls										
mean/day	505.14	101.59	25.14	149.98	167.16	36.33	94.05	457.39	106.74	168.59
min/max	0/2332	0/841	0/312	0/1363	0/772	0/202	0/502	0/1556	0/384	0/1183
CV	529.43	157.25	213.19	172.68	102.18	143.69	126.25	73.29	94.54	130.72
Duration										
mean/day	71.96	44.18	18.56	48.57	52.67	24.35	43.32	68.02	36.12	36.45
min/max	1/168	0/157	0/84	0/122	0/110	0/92	1/104	1/151	0/90	0/99
CV	46.19	94.56	114.79	65.82	41.10	96.10	55.82	44.25	55.57	70.15

Table 2.2. Proportions of audio, audio-visual (AV), and silent-visual (SV) detections of Marbled Murrelets recorded during surveys at five survey stations, Oregon Coast Range, 1 May - 5 August, 1994, 1996, 1997. n = number of survey days.

	Survey stations									
	2x4	SCMF		SCUF	VGM			VGUP		
	‘97	‘94	‘97	‘94	‘94	‘96	‘97	‘94	‘96	‘97
Detection type	(n=62)	(n=66)	(n=61)	(n=58)	(n=55)	(n=50)	(n=58)	(n=55)	(n=51)	(n=56)
% audio	53.47	11.17	30.36	69.75	60.92	73.40	64.97	79.44	79.28	61.49
% AV	16.13	17.45	7.67	12.95	15.51	3.19	12.99	9.65	8.07	19.54
% SV	30.40	71.38	61.97	17.30	23.57	23.40	22.03	10.91	12.66	18.97
No. detections	3260	2086	639	942	1502	376	885	1980	719	870

mum values for daily counts of detections, keer calls, and occupied detections were 3 to 8 times, 3 to 9 times and 3 to 15 times greater than the means, respectively, among sites and years.

Temporal and Spatial Variability in Activity

Each daily activity metric was highly variable within and among sites and years. Counts of daily keer calls and occupied detections were the most variable metrics; duration of activity was always the least variable metric (Table 2.1). A closer examination of number of daily detections, the primary activity metric, revealed an inconsistent pattern of variability within and among sites and years (Fig. 2.3). For example, month-by-month estimates of coefficients of variation (CVs) for daily detections at all stations during all years ranged from 38% - 210% (Table 2.3). We could not identify any month when CVs were consistently higher or lower than any other month. Similar temporal variability occurred for each activity metric.

Correlation among the four daily activity metrics was moderate to strong within each site each day ($0.535 < r_s < 0.875$). However, correlation between identical activity metrics from proximal survey stations on the same day were often not very similar (Table 2.4). Furthermore, correlative strength of weekly means for each activity metric varied greatly among survey stations ($-0.423 < r_s < 0.797$) and proximity of survey stations was not necessarily indicative of correlative strength. For example, weekly means of each activity metric were always most strongly correlated between proximal stations in 1994, but typically least correlated between proximal stations in 1997. Seasonal timing of activity also appeared to vary among years within stations. Correlation coefficients were weak to moderate within sites among years for daily detections ($-0.462 < r_s < 0.475$), duration of daily activity ($-0.186 < r_s < 0.482$), and proportion of occupied detections/day ($-0.126 < r_s$

Figure 2.3. Daily counts of Marbled Murrelet detections recorded at five inland survey stations in the Oregon Coast Range, 1 May – 5 August 1994, 1996, 1997.

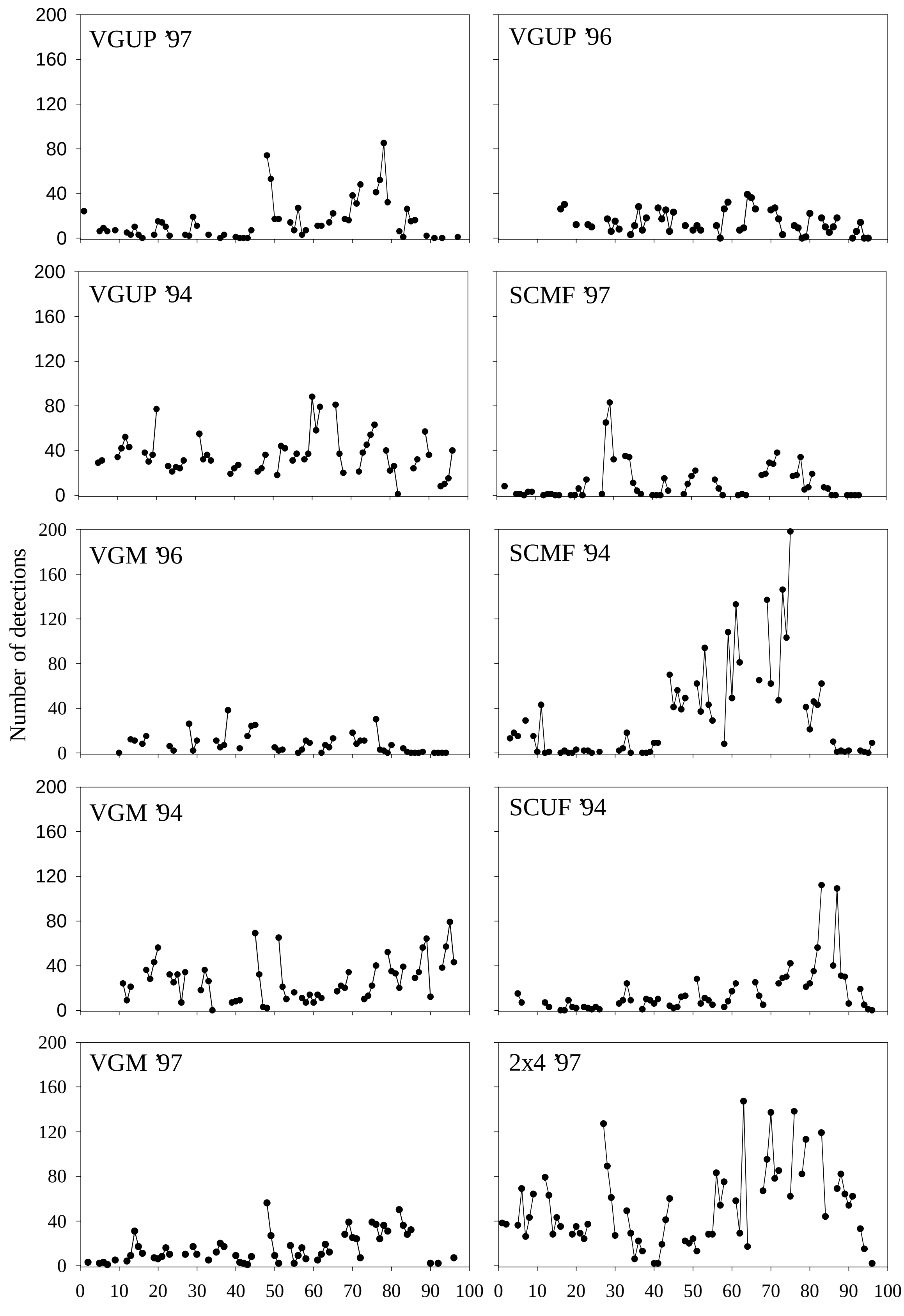

VGUP '97
VGUP '96
VGUP '94
SCMF '97
VGM '96
SCMF '94
VGM '94
SCUF '94
VGM '97
2x4 '97
Number of detections
0
40
80
120
160
200
0 10 20 30 40 50 60 70 80 90 100
Day number (1 May = day 1)
Day number (1 May = day 1)

Figure 2.3

Table 2.3. Monthly coefficients of variation for counts of daily Marbled Murrelet detections recorded during surveys at five survey stations in the Oregon Coast Range, 1 May - 31 July, 1994, 1996, 1997.

	Coefficients of Variation									
	2x4	SCMF		SCUF	VGM			VGUP		
	'97	'94	'97	'94	'94	'96	'97	'94	'96	'97
May	53.61	153.04	210.13	98.01	47.31	82.52	77.23	38.70	53.50	79.82
June	72.82	95.44	111.53	72.13	104.12	98.38	107.71	46.34	64.80	147.29
July	44.63	94.47	107.34	81.55	52.96	131.94	53.63	54.05	80.29	85.27
May - July	69.51	130.00	152.46	134.08	68.40	113.43	87.44	49.30	72.09	121.65

Table 2.4. Spearman correlation coefficients among Marbled Murrelet activity metrics recorded on the same day at proximal survey stations in the Oregon Coast Range, 1 May - 5 August, 1994, 1996, 1997.

Proximal survey stations		No. survey days[1]	Spearman Correlation Coefficient		
			detections	keer calls	duration (min)
SCUF '94	SCMF '94	54	0.426	0.508	0.430
VGM '94	VGUP '94	50	-0.103	-0.036	0.584
VGM '96	VGUP '96	44	0.507	-0.379	0.641
VGM '97	VGUP '97	50	0.436	0.083	0.274

[1] Number of days both stations were surveyed simultaneously.

< 0.455).

Relationships Between Activity and both Weather and Date

The degree of weather-related visibility at a stand, represented by the summed variable of cloud, ceiling and fog (CLCEFO), differed significantly among months (ANOVA $F_{2,518} = 7.82$, $P < 0.001$) but not among sites (ANOVA $F_{4,518} = 0.01$, $P = 1.0$) or site*month interactions (ANOVA $F_{8,518} = 0.54$, $P = 0.83$). Tukey-Kramer post-hoc comparisons revealed that July was clearer (i.e., cloud and fog cover less, ceiling higher) than May or June. August was not included in these analyses due to low sample size (i.e., < 5 survey days/site/yr).

Weather and date variates explained little of the variability in Marbled Murrelet activity (Table 2.5). Although canonical correlation coefficients (CC) between the first independent and dependent variates were moderate to strong, the canonical redundancy indices (CRIs) indicated these first CCs explained <21 % of the variability in the activity data at all but 1 survey station (Table 2.5). The second CCs explained < 6.2 % of the variability. Based on the strength of CC, CRI, and likelihood ratio *P*-values we chose to interpret the structure of the first and second canonical correlations at the 2x4, SCUF, and VGUP stations and the first canonical correlations at SCMF and VGM.

The canonical loadings (CLs; Table 2.6) show the influence of each weather and date variable on the independent variate. The interpretation for V1 varied among survey stations based on these loadings. V1 had a strong weather influence at 2x4, a strong date (i.e., month or year) influence at SCMF, SCUF, and VGUP, and a moderate influence from all variables at VGM. The strongest CLs for V1 for any site were date influenced (month at SCUF and year at VGUP) while the weakest CLs were CLCEFO at SCMF and month at VGUP (Table 2.6).

Table 2.5. Canonical correlation coefficients, likelihood ratio *P* values, and canonical redundancy indices for the first three canonical variates between daily Marbled Murrelet activity metrics and both weather and date variables at five survey stations, Oregon Coast Range, 1 May - 31 July, 1994, 1996, 1997.

Survey station	Canonical correlation no.[1]	Canonical Correlation coefficent	Likelihood ratio *P*- value[2]	Canonical Redundancy Index[3]
2x4	*1*	0.631	0.001	0.096
	2	0.552	0.002	0.062
	3	0.126	0.645	0.009
SCUF	*1*	0.747	0.001	0.444
	2	0.434	0.042	0.013
	3	0.249	0.216	0.008
SCMF	*1*	0.476	0.001	0.204
	2	0.251	0.195	0.002
	3	0.191	0.256	0.002
VGM	*1*	0.293	0.110	0.057
	2	0.195	0.375	0.010
	3	0.139	0.408	0.001
VGUP	*1*	0.492	0.001	0.206
	2	0.402	0.001	0.013
	3	0.107	0.634	0.001

[1] Italicized correlation numbers indicate canonical correlation and canonical redundancy indices that were considered significant enough ($P \leq 0.10$) to be further evaluated (see Table 6).
[2] The likelihood ratio tests the null hypothesis that the canonical correlation values in the current row and all that follow are 0.
[3] The canonical redundancy index (CRI) equals the mean proportion of canonical cross-loadings. The CRI represnets the proportion of variance in the dependent variables explained by the independent variate.

Table 2.6. Canonical loadings and canonical cross-loadings from canonical correlation analyses between daily Marbled Murrelet activity metrics and both weather and date variables recorded during surveys at five survey stations, Oregon Coast Range, 1 May - 31 July, 1994, 1996, 1997.

	2x4		SCMF	SCUF		VGM	VGUP	
Canonical Loadings								
	V1[1]	V2	V1	V1	V2	V1	V1	V2
clcefo[2]	0.657	-0.210	0.027	-0.248	0.089	0.526	0.330	0.731
Month	0.156	0.964	0.589	0.957	0.250	-0.372	0.050	-0.652
Precip.	0.668	-0.308	0.187	-0.349	0.818	0.239	-0.321	0.357
Wind	0.639	0.215	0.170	-0.149	-0.136	0.417	0.164	-0.584
Year[3]	n/a	n/a	-0.697	n/a	n/a	-0.649	-0.947	0.114
Canonical Cross-loadings								
	2x4		SCMF	SCUF		VGM	VGUP	
	U1[4]	U2	U1	U1	U2	U1	U1	U2
Detects.	0.116	0.195	0.457	0.736	0.067	0.244	0.486	-0.015
Keers	0.173	0.368	0.467	0.702	-0.086	0.194	0.446	0.014
Duration	0.495	0.109	0.431	0.546	0.168	0.274	0.428	0.195

[1] V1 = first independent variate, V2 = second independent variate.
[2] clcefo = combnined weather variable cloud, ceiling and fog.
[3] n/a = sites with only one year of data; year not available for inclusion in model.
[4] U1 = first dependent variate, U2 = second dependent variate.

Canonical cross-loadings (CXLs, U1 and U2; Table 2.6) demonstrate the correlation strength between each activity metric and the independent variate (e.g., V1). CXLs were the most uneven at 2x4 where they indicated that V1 (predominantly a weather effect) had a greater effect on duration of activity (explaining about 25% of its variability, i.e., CXL^2) than the other activity metrics. The dependent activity metrics were more evenly correlated with the independent variates within each of the remaining survey stations. At both SC stations, V1 (predominantly effects of month and year) explained 18% - 54% of the variability in activity metrics. At VGM, V1 (a mixed weather and date effect) explained only 3.7% - 7.5% of the variability in each activity metric while at VGUP, V1 (a strong year effect) explained 18.3% - 23.6% of the variability in each activity metric. The proportion of variability in the activity metrics explained by V2 varied from < 1% - 13.5%. The strongest correlation between activity metrics and V1 occurred at SCUF where V1 was predominantly a month effect. The weakest correlation between activity metrics and V1 occurred at 2x4 where V1 was predominantly a weather effect.

We also conducted canonical correlation analyses without year or month as independent variables in an effort to maximize the potential of observing a significant or consistent relationship between weather and activity. However, results still indicated only a weak relationship between activity and weather. Only 2 of the 10 site*year combinations had first canonical correlations significantly different from zero (i.e., likelihood ratio *P* values < 0.05). The range of variability in activity data among all survey stations explained by the weather-loaded independent variates (i.e., CRI) was 1 - 13%. The maximum CRI occurred at VGUP '94 and the strongest correlation within that station was between CLCEFO and duration of activity (CL for CLCEFO = 0.79, CXL between V1 and duration = 0.44).

Results from analyses of occupied detections were similar to those of other activity metrics. There was no correlation between weather (i.e., CLCEFO), and either the proportions of occupied detections/day or the number of occupied detections/day for any site in any year ($-0.235 < r_s < 0.144$). The percent of occupied detections/day was significantly different among years at sites with multiple years of data (Kruskal-Wallis $P <$ 0.038 for each site) and the proportion of occupied detections/day was greatest in 1994 and least in 1996 at each station. Month had an inconsistent effect on the proportions of occupied detections/day among sites and years (Table 2.7). Furthermore, no two stations with significant month effects shared the same monthly ranking for proportions of occupied detections/day. VGM '96 and VGM '97 had opposite rankings.

We examined daily patterns of detections (Fig. 2.3) and smoothed versions of these same data (Fig. 2.4) to evaluate seasonal and inter-annual trends in activity. We restricted these analyses to one metric since correlations between all daily activity metrics were high ($r_s >$ 0.7). We chose counts of daily detections as it is the metric most likely to be considered important for monitoring purposes. Maximum or near-maximum numbers or daily detections occurred throughout the breeding season and near-minimum and maximum detection values were often recorded during the same week within a site (Fig. 2.3). Ranking the five highest detection days/site and sorting these by date revealed that 12% of these maximum or near-maximum detection days occurred in May, 46% occurred between 1 June and 9 July, and 42% occurred between 10 July and 5 August. (These dates were chosen to reflect date-specific survey effort suggested in the Marbled Murrelet survey protocol; Ralph et al. 1994). However, a LOWESS smoothing analysis (tension = 0.2) of daily detection data revealed an underlying pattern where overall activity began to peak in late June at most sites during most years (Fig. 2.4). Additionally, most sites also showed secondary peaks in activity that did not consistently occur during any week or month of the survey. The smoothed data also showed activity patterns to be slightly more similar among survey stations within years than previous correlation analyses; however, proximal stands did not always display the most similar patterns within years.

Table 2.7. Median proportion of Marbled Murrelet occupied detections/day between 1 May and 31 July, 1994, 1996, 1997, at five survey stations in the Oregon Coast Range and results from Kruskal Wallis analysis testing for differences in proportion of occupied detections/day by month at each survey station. n = number of survey days.

	Survey stations									
	2x4	SCMF		SCUF	VGM			VGUP		
	‘97 (n=62)	‘94 (n=66)	‘97 (n=61)	‘94 (n=58)	‘94 (n=55)	‘96 (n=50)	‘97 (n=58)	‘94 (n=55)	‘96 (n=51)	‘97 (n=56)
May	32.43	64.44	00.00	00.00	38.89	12.50	00.00	13.63	06.67	00.00
June	39.68	81.63	77.27	50.00	21.11	08.54	11.11	18.74	09.09	18.25
July	33.87	84.83	78.97	19.35	19.23	00.00	20.51	15.38	25.93	20.91
Kruskal wallis *P* - value	0.267	0.121	0.007	0.009	0.198	0.011	0.008	0.412	0.156	0.101

Figure 2.4. Counts of daily Marbled Murrelet detections (plotted as the proportion of the annual maximum number of detections at respective sites to standardize trends among stations) recorded at five inland survey stations in the Oregon Coast Range, 1 May – 5 August 1994, 1996, 1997. Smoothed lines derived with locally weighted regression (LOWESS; tension = 0.2); symbols for each day are not included to improve clarity but are shown in Figure 2.3.

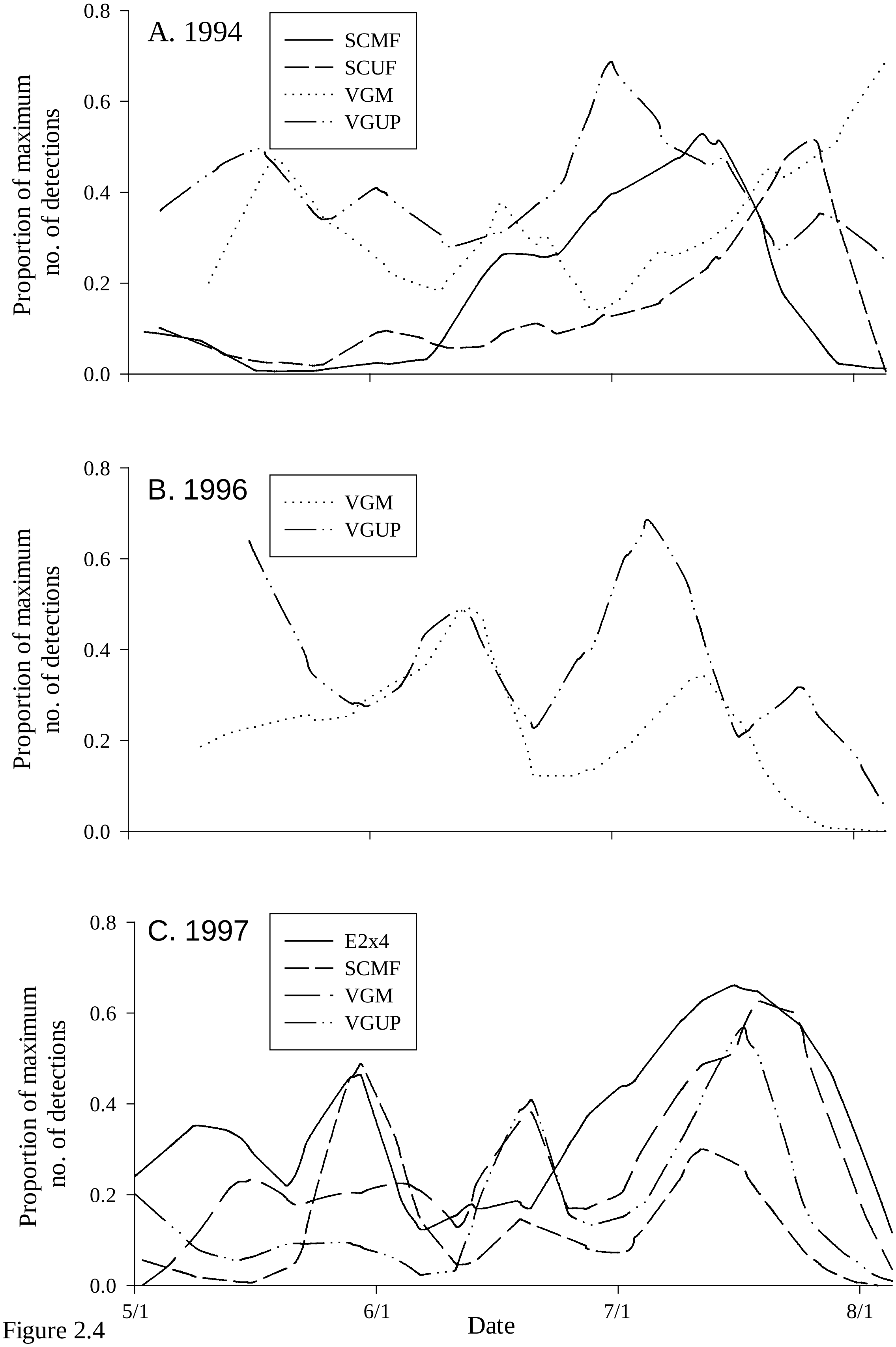
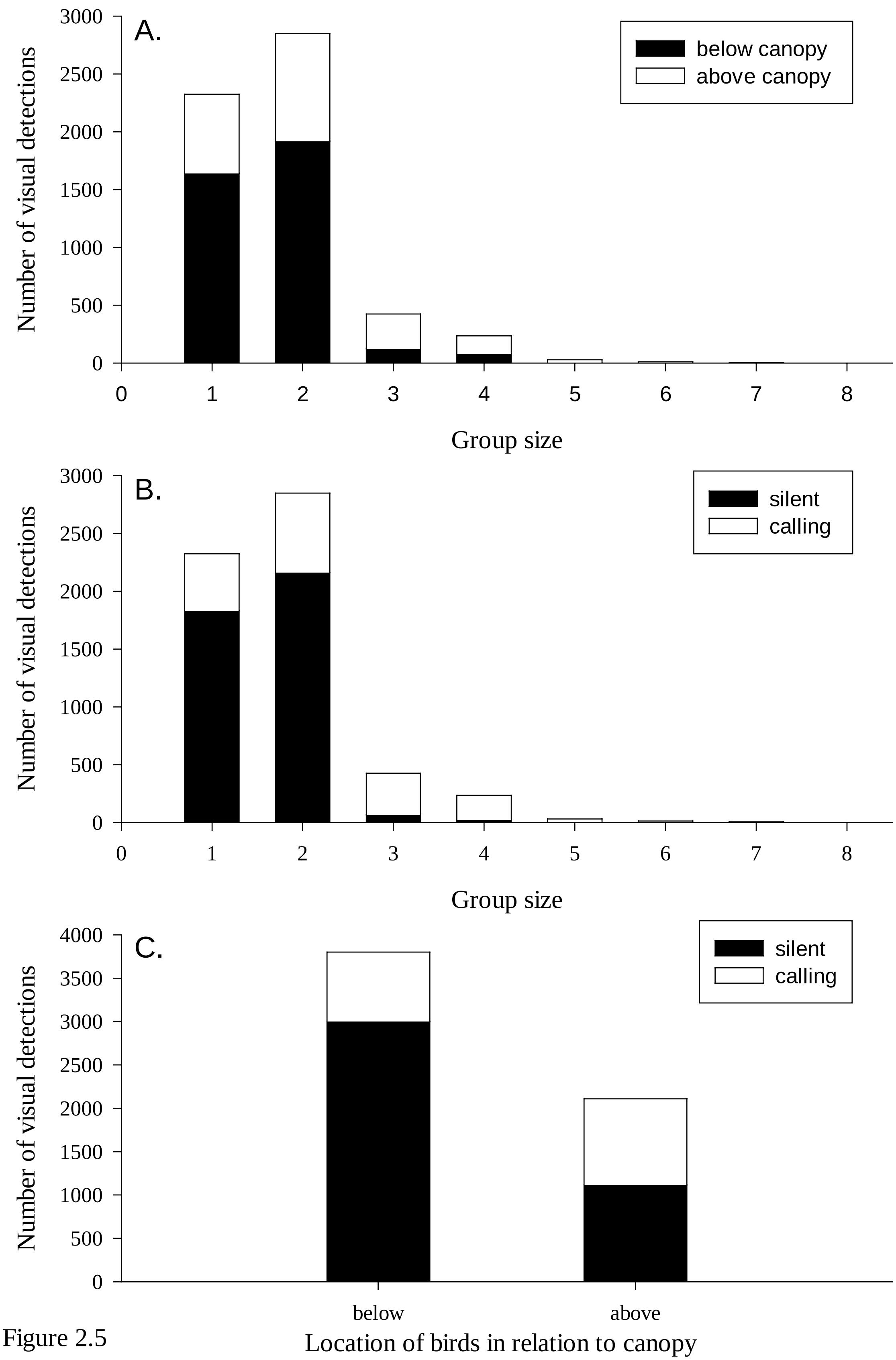

A. 1994
SCMF
SCUF
VGM
VGUP
B. 1996
VGM
VGUP
C. 1997
E2x4
SCMF
VGM
VGUP
Proportion of maximum no. of detections
0.0
0.2
0.4
0.6
0.8
5/1
6/1
7/1
8/1
Date

Figure 2.4

Behavior and Group Size

Most Marbled Murrelet groups observed at inland forest stands consisted of 1 or 2 birds (mean pooled from visual detections = 1.78, sd = 0.83). Smaller groups typically occurred below canopy and were silent while larger flocks tended to occur above the canopy and were calling (Fig. 2.5). Although the final generalized linear models for group size included a slightly different set of variables for each survey area (Table 2.8), some patterns within the explanatory variables were consistent. Group size was most strongly affected by flight height and type of behavior at all survey areas (Table 2.8; *F* values); average group size increased by about 1.1 birds/group at each survey area when murrelets were detected above canopy versus below canopy and by about 1.3 birds/group when murrelets were calling versus silent (Table 2.9; mean responses). Group sizes increased between time period two and three at all three areas; however, the relationship between time of day and group size varied among sites for comparisons among time periods three through five (Table 2.9). There appeared to be little variation in average group size by month when data were pooled among all areas; average group sizes for May, June, and July were 1.71, 1.70, and 1.86, respectively. Similarly, group size was significantly related to month only at the 2x4 site. At a larger time scale, group size was significantly affected by year (only considered at the VG sites; Table 2.9). There were about 1.2 more birds/group in 1994 than 1996 and about 0.8 fewer birds/group in 1996 than 1997. Average group sizes were always less than two each year, however (1994: mean = 1.67, sd = 0.79; 1996: mean = 1.47, sd = 0.69; 1997: mean = 1.82. sd = 0.86).

Figure 2.5. Frequency of visual Marbled Murrelet detections by: a) group size and height in relation to canopy; b) group size and detection type (audio-visual or silent-visual), and; c) detection type and height in relation to canopy. Detections, recorded at five inland survey stations in the Oregon Coast Range, 1994, 1996, and 1997, pooled among all sites and years.



A.
below canopy
above canopy
Number of visual detections
3000
2500
2000
1500
1000
500
0
0
1
2
3
4
5
6
7
8
Group size
B.
silent
calling
Number of visual detections
3000
2500
2000
1500
1000
500
0
0
1
2
3
4
5
6
7
8
Group size
C.
silent
calling
Number of visual detections
4000
3500
3000
2500
2000
1500
1000
500
0
below
above
Location of birds in relation to canopy

Figure 2.5

Table 2.8. Final Poisson regression models for visual detections of Marbled Murrelets with flock size as the response variable. Model selection process was forward, single-best-predictor with an *F* to enter of 4.0; final models were selected based on drop-in-deviance tests and Bayesian information criteria. Survey data collected at five survey stations, Oregon Coast Range, 1 May - 31 July, 1994, 1996, 1997.

		Valley of the Giants (VGM & VGUP) (ddf = 1791)[a]		Spencer Creek (SCMF & SCUF) (ddf = 2116)		2x4 (ddf = 1493)	
Explanatory variable	Num. Df[a]	*F*	*P*	*F*	*P*	*F*	*P*
Detection type	1	180.18	0.0001	175.17	0.0001	335.04	0.0001
Detection ht.	1	30.99	0.0001	27.65	0.0001	19.50	0.0001
Month	2	n/s [b]		n/s		15.22	0.0001
Time of day	4	22.91	0.0001	61.11	0.0001	15.82	0.0001
Year	2	20.59	0.0001	n/a [b]		n/a	

[a] Num. df = numerator degrees of freedom; ddf = denominator degrees of freedom.
[b] n/s = variable not selected for final model for that survey area; n/a = variable has only one level and was not available for inclusion in the model.

Table 2.9. Poisson regression model estimates of the mean change (with 95% confidence intervals)[1] in group size of Marbled Murrelets at each of three survey areas when visual detections occur in the indicator level versus the reference level for each explanatory variable (e.g., a mean response <1 indicates mean group size decreases by that amount in the indicator level). n = number of visual detections used in each survey area's Poisson regression model.

Explanatory variable	Reference level	Indicator level	VG mean response (95% lci,uci) (n=1801)	SC mean response (95% lci,uci) (n=2124)	2x4 mean response (95% lci,uci) (n=1503)
Height of detection	above canopy	below canopy	*0.891* (0.855,0.928)	*0.890* (0.852,0.929)	*0.902* (0.862,0.945)
Month	June	May	n/s[2]	n/s	*0.907* (0.857,0.959)
	July	June	n/s	n/s	0.970 (0.913,1.031)
Time period	3	2	*0.871* (0.830,0.913)	*0.833* (0.800,0.867)	*0.834* (0.788,0.883)
	4	3	*0.908* (0.857,0.962)	*0.886* (0.846,0.928)	1.034 (0.973,1.098)
	5	4	1.034 (0.955,1.121)	1.011 (0.962,1.062)	0.924 (0.862,1.011)
Type of detection	visual-silent	visual-audio	*1.318* (1.266,1.377)	*1.270* (1.227,1.315)	*1.496* (1.433,1.561)
Year	96	94	*1.198* (1.124,1.278)	n/a[2]	n/a
	97	96	*0.818* (0.767,0.871)	n/a	n/a

[1] A 95% confidence interval that includes 1.0 indicates that the change in mean response is not significant (i.e., flock size is not affected by that explanatory variable). Italicized values indicate CI that do not contain 1.0 (i.e., are significant).
[2] n/s = variable not selected for final Poisson regression model for that survey area; n/a = variable has only one level and so is not available for inclusion in the Poisson regression model.

DISCUSSION

Spatial and Temporal Variability of Activity

The daily timing of Marbled Murrelet activity and relative proportions of types of detections we recorded were similar to those reported elsewhere for this species (see Naslund and O'Donnell 1995). However, we observed greater variability in Marbled Murrelet activity levels than has been previously reported for this species (Rodway et al. 1993) or for other alcids (Jones et al. 1990, Piatt et al. 1990). For example, Rodway et al. (1993) reported CVs of 20 - 90% for Marbled Murrelet all daily activity metrics throughout the breeding season, while we reported CVs for these same measures as high as 500% for certain metrics.

Monthly patterns of CVs for Marbled Murrelet daily activity also appeared to be inconsistent among our sites. There was no evidence that CVs were typically higher or lower during any given month when data were examined across all sites and years. Similarly, Rodway et al. (1993) also documented differences in variability of activity among months for Marbled Murrelets in British Columbia. Similar temporal variability in attendance patterns also have been reported for Ancient Murrelets (*Synthliboramphus antiquus*), and Thick-billed Murres (*Uria lomvia*; Gaston and Nettelship 1982, Jones et al. 1990).

Daily activity levels of Marbled Murrelets among forest stands also appear to be highly variable. Rodway et al. (1993) observed an inconsistent relationship between identical activity metrics on the same day at two nearby stands; our data showed a similar tendency at the daily, weekly, and annual scales. Weather conditions at the nest stand and breeding phenology each have been suggested as factors that might affect variability in activity patterns of Marbled Murrelets (see reviews in Naslund and O'Donnell, 1995, and

O'Donnell et al. 1995); the relationship of each of these factors to activity are discussed in turn.

Weather and Activity

Marbled Murrelet activity is thought to increase with increasing local cloud or fog cover (see Naslund and O'Donnell 1995). However, most data used to infer this relationship may be misleading because they were not collected from observational experiments specifically designed to test this relationship. Surveys specifically designed to test the relationship between activity and weather have shown inconsistent relationships. Rodway et al. (1993) found duration of murrelet activity significantly increased on days with >80% cloud cover at both of their survey sites, counts of detections significantly increased on days with >80% cloud cover at only one site, and no significant relationship between heavy cloud cover and keer calls at either site. Preliminary analyses from northern California also suggest a weak relationship between activity levels and weather conditions (Ralph pers. comm.). My results also showed relatively weak and inconsistent relationships between weather and levels of Murrelet activity. Direct comparisons with Rodway et al. (1993) are difficult, however, as our analyses included more detailed explanatory variables to account for weather.

We found minimum, moderate, and near-maximum levels of detections occurred across the entire range of cloud cover conditions, but the absolute maximum levels of activity always occurred on overcast days. We also determined that when weather was a significant factor, duration of activity was affected more than counts of detections or counts of keer calls. These observations, taken together with those of Rodway et al. (1993), suggest that activity may be high or low in any cloud cover condition but maximum activity days tend to occur during very overcast conditions. Therefore, the relationship between activity levels of Marbled Murrelets and weather is not consistent or strong. Furthermore, if weather were the primary factor influencing Murrelet activity levels at inland forest sites, then intra-annual trends in activity should be similar at proximal survey stations. The lack of a strong correlation between identical activity metrics at proximal stations on the same day during our study suggests otherwise.

Date, Breeding Phenology, and Activity

Breeding phenology may affect seasonal patterns in Marbled Murrelet activity. Many alcids display high and highly variable attendance during early breeding (pre-laying), lowered attendance and variability during incubation, and increased and often highest attendance and variability during chick hatching and colony departure (Gaston and Jones 1998). For example, for Least Auklets (*Aethia pusilla*) Piatt et al. (1990) recorded daily attendance CVs of 549% during chick rearing but CVs < 200% during incubation. Based on the limited data available for Marbled Murrelet breeding phenology it appears our observations of seasonal patterns in activity shared some characteristics with those described for other alcids. Activity at our sites typically increased in July, when fledging likely peaks for murrelets in Oregon (Nelson and Hamer 1995). We observed lesser increases in activity earlier in the season but the timing varied among stations and years from very early May (e.g., VGUP ’94, 2x4 ’97) to mid-June (e.g., VGM ’96). Lowest levels of activity often occurred in June at most sites during most years, which likely coincides with incubation (Nelson and Hamer 1995).

The few data available on Marbled Murrelet breeding phenology indicate that timing of breeding stages may vary widely. Fledging ranges from mid-June through mid-September in Washington, Oregon, and California (Hamer and Nelson 1995) and such a range in phenology may account for some of the variability observed in activity patterns among sites and years. However, survey data from our study clearly show activity can vary greatly from one day to the next during any portion of the breeding season and it is unlikely that such erratic patterns are due to changes in breeding phenology alone.

Chick feeding also may increase activity levels of Marbled Murrelets at nesting stands. Piatt et al. (1990) documented an increase in total movement of Least Auklets at a colony of two- to fourfold during chick rearing. Nelson and Hamer (1995) report adult Murrelets feed chicks up to 8x/day. If both adults visited a nest to feed a chick twice during the survey period (which extends typically to 75 minutes post-sunrise) this would increase counts of detections only fourfold. It is unlikely that chick feeding alone could account for an eight- to tenfold increase in activity on subsequent days as was often observed (e.g., SCUF in 1994, 2x4 in 1997). Therefore, chick feeding could account for some proportion of increased activity later in the breeding season (i.e., likely after late June) but probably not peaks in activity observed during May or most of June.

While weather and breeding phenology may account for some of the variability and underlying patterns observed in Marbled Murrelet activity, it is still unclear which factors are responsible for the extreme daily and annual variability that occurs in activity within each survey station. For example, we observed strong negative trends in activity among years at each station where >1 year of data were collected, indicating strong variability in activity among years. On a shorter time scale we often observed successive days of activity ranging from annual minimum or near-minimum levels to maximum levels and back to near-minimum levels (e.g., 2x4 in 1997, SCMF in 1994); Jones et al. (1990) noted a similar activity pattern for Ancient Murrelets in British Columbia. In other seabirds, differences in the magnitude of annual attendance and daily variability in attendance within a year have been attributed at least in part to irregular attendance patterns of nonbreeders, (e.g., Gaston and Nettleship 1982, Jones et al. 1990, Nelson 1987). For example, nonbreeders have been estimated to account for up to 23% of the Pigeon Guillemots (*Cepphus columba*) attending a colony during pre-laying (Ewins 1985), up to

50% of Cape Petrels (*Daption capense*) attending a colony during incubation (Weidinger, 1996), and up to 50% of Least Auklets attending a colony during incubation (Piatt et. al. 1990).

Variability in the numbers of nonbreeding alcids attending colonies has been attributed to daily, seasonal, and annual changes in foraging conditions (Gaston and Nettelship 1982, Nelson 1987, Jones et al. 1990). It is likely that when foraging conditions improve, foraging consumes a smaller proportion of an individuals daily activity budget and individuals would thus have more time to invest in colony visits. While we have no direct evidence of links between foraging conditions and levels of Marbled Murrelet activity at inland nest sites, we did observe a moderate yet significant negative correlation ($r_s = -0.47$) between the mean number of daily detections at the two VG sites in 1996 and the percent time spent underwater (i.e., foraging) during a foraging bout by telemetered Marbled Murrelets offshore of those survey stands on the same day. We also observed that duration of dive bouts increased in 1996 for these same telemetered birds. Therefore as birds increased foraging bout duration and spent more time diving during a foraging bout and less time resting (i.e., as energy expended during a bout increased), there were appeared to be fewer detections at VGM and VGUP. While these observations are not conclusive, they do suggest a relationship between activity and foraging behavior.

On a larger time scale, Nelson (1987) attributed higher annual attendance of nonbreeding Pigeon Guillemots to improvements in foraging conditions. Similarly we observed the average and maximum numbers of Marbled Murrelet detections at VG during each survey year appeared to parallel marine foraging conditions (as determined by sea surface temperature; SST). Detections were lowest (mean and maximum measures) during 1996, when SST along the central Oregon coast was highest for the three survey years, and when a nearby Common Murre (*Uria aalgae*) colony experienced early abandonment (Lowe pers. comm.); detections were highest in 1994 when SST was lowest. These observations suggest that foraging conditions may affect the numbers of birds attending forest stands and that the effect of foraging conditions may extend to breeders (differences in average detection rate among years) and nonbreeders (maximum numbers of detections within and among years).

The lack of a consistent relationship between activity peaks among regions (e.g., VG versus SC) at either the daily or weekly scale might be accounted for by regional differences in foraging conditions or breeding phenology. However, the lack of a strong or consistent correlation in activity peaks at proximal stands at the weekly or daily scale and the lack of similarity in smoothed activity patterns at proximal stands (e.g., compare similarity in VGM and VGUP in 1996 with VGM and VGUP in 1994; Fig. 2.4) would not explain differences in foraging conditions for attending birds. We would suspect that birds attending proximal stands would forage in similar marine locations and thus experience similar large-scale foraging conditions. This inconsistent correlation between activity at nearby stands suggests that, if it is the proportion of nonbreeding birds that accounts for activity peaks, then nonbreeding Marbled Murrelets may vary which stands are visited on a given day. This might account for the weak and inconsistent daily correlation between activity metrics at proximal survey stations. Rodway et al. (1993) also failed to document a consistent or strong daily activity correlation between nearby stands.

Behavior and Group Size during Detections

Marbled Murrelet behavior at inland forest stands appears to be similar across much of their range. For example, maximum group sizes reported from California to British Columbia vary only from 6 - 8 and average group sizes from these regions all are slightly less than 2 (Rodway et al. 1993, Manley et al. 1992, O’Donnell et al. 1995). Similarly, most studies including ours indicate that Murrelets detected below canopy tended to be silent and occur as singles or pairs, while birds detected above the canopy tended to vocalize and occur as groups of two or more. Observations at Marbled Murrelet nests indicate that nesting adults typically approach and depart the nest silently (Nelson and Peck 1995). Nesting adults of other alcids also tend to approach the nest silently and directly and this is likely done to avoid predation (Gaston and Jones 1998). Therefore, detections of single, silent birds below the canopy are most likely to reflect actively nesting Murrelets and therefore may provide the most accurate information about activity patterns and behavior of nesting birds.

The significant increase in group size with time of day also may be due to nesting behavior. Singer et al. (1995) and Nelson and Peck (1995) report that nesting adults tend to arrive at the nest site singly and during the earliest portions of the surveys. Raptors have been observed attacking and capturing adult Marbled Murrelets in nesting stands (Marks and Naslund 1994, Carter pers. comm.) and it is likely that these secretive behaviors are a response to that predation pressure. Larger groups during the middle and late portions of the survey period may therefore be comprised of non-breeding adults that are displaying or prospecting.

Average group sizes appeared to vary among years within our sites, a behavioral change yet to be reported for this species. Group sizes at VG were least during 1996 which, of the three years we surveyed, likely represented the year of poorest foraging conditions at sea. Estimates of mean detections/day at the VG stations also were lowest during 1996. If nonbreeding birds make up a significant proportion of birds attending nest stands, as has been demonstrated with other alcids and as discussed previously, and if the proportion of nonbreeding birds attending nest sites is directly related to foraging quality at sea, then lowered average group sizes in 1996 may be due in part to fewer nonbreeding birds attending the forest stands. This effect on group size would be consistent with other differences in activity patterns noted during 1996.

This study indicates that Marbled Murrelet activity is highly variable at all temporal and spatial scales, and that activity patterns may be more variable than previously reported. However, it remains unclear why the correlation between activity and weather was inconsistent among survey stations and what role, if any, nonbreeding birds played in contributing to variability in activity during the breeding season. Given the extreme levels of variability present in Marbled Murrelet activity data and our lack of understanding as to which factors drive that variability, it is critical not to draw conclusions about Marbled Murrelet activity or behavior from small data sets or data sets not specifically designed to answer the questions of interest. Further study of Marbled Murrelet activity using RADAR, and a direct comparison of simultaneously collected RADAR and observer-based surveys with intensive samples from a single station (e.g., >20 survey days), would provide valuable information on the accuracy of observer-based survey efforts and their potential usefulness in describing and understanding Murrelet behavior at forest stands. Studying activity patterns of telemetered birds in and around nest stands also would provide valuable information on daily activity patterns and behavior during flight. Additional multi-year, daily or near-daily survey efforts such as ours are needed throughout the species' range; to date only one other similar study has been conducted (Rodway et al. 1993). These daily or near-daily activity data can be used to determine how visitation at nesting areas varies spatially and temporally and how these patterns are affected by forest conditions and marine foraging conditions. Data sets from less intensive survey efforts scattered over many stands and collected by multiple observers at each survey station may in fact provide misleading information.